A Supraspecific Classification of the Scaphopod Mollusca

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(4 Text figures)

INTRODUCTION

In a series of papers (1951 - 1958) W. K. Emerson unravelled a formidable tangle of taxonomic problems in the nomenclature of the scaphopod molluscs. His work culminated in a "Classification of the scaphopod mollusks" (Emerson, 1962) which, because of its stable nomenclatural foundation, was a great advance on that previously proposed by Pilsbry & Sharp (1897 - 1898). Nevertheless, attempts by the present writer to apply Emerson's systematic arrangement presented many difficulties which were only resolved by a reassessment and redistribution of the taxonomic units within it. Emerson's classification may be summarised thus:

Class SCAPHOPODA Bronn, 1862

Family Dentaliidae Gray, 1847

- *Prodentalium*
- *Dentalium* (s. s.) — *Dentalium* sensu lato
- *Coccodentalium* — *Dentalium* sensu lato
- *Fissidentalium* — *Dentalium* sensu lato
- *Tesseracme* — *Dentalium* sensu lato
- *Graptacme* — *Dentalium* sensu lato
- *Antalis* — *Dentalium* sensu lato
- *Plagioglypta*
- *Gadilina* — *Fustiaria* sensu lato
- *Lobantale* — *Fustiaria* sensu lato
- *Bathoxifus* — *Fustiaria* sensu lato
- *Compressidens* — *Fustiaria* sensu lato
- *Episiphon* — *Fustiaria* sensu lato
- *Laevidentalium* — *Fustiaria* sensu lato
- *Fustiaria* (s. s.) — *Fustiaria* sensu lato
- *Rhabdus* — *Fustiaria* sensu lato

Family Siphonodentaliidae Simroth, 1894

- *Entalina*
- *Siphonodentalium*
- *Pulsellum*
- *Cadulus* (s. s.) — *Cadulus* sensu lato
- *Gadila* — *Cadulus* sensu lato
- *Striocadulus* — *Cadulus* sensu lato
- *Dischides* — *Cadulus* sensu lato
- *Polyschides* — *Cadulus* sensu lato
- *Platyschides* — *Cadulus* sensu lato

Three main objections to this system of classification may be raised:

1) the ordinal rank is unoccupied;
2) the taxa "*Fustiaria* sensu lato" and "*Dentalium* sensu lato" function as if they were at the family level in collectively acting as 'umbrella' to 14 generic groups;
3) too many large and distinct groups are only accorded the status of subgenera.

These objections will be supported by arguments in the following discussion.

SCAPHOPODA

DENTALIOIDA SIPHONODENTALIOIDA

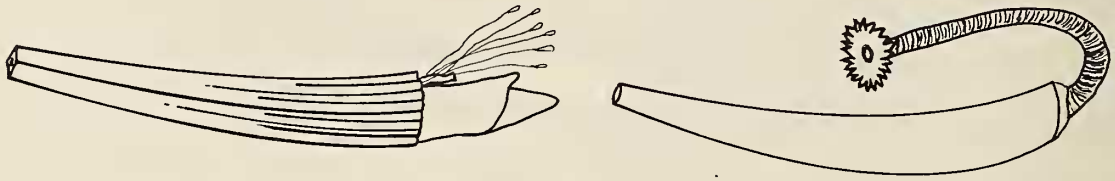

Figure 1

The primary divisions of the class Scaphopoda into:
order Dentalioida, animal with conical foot, and
order Siphonodentalioida, animal with vermiform foot and distal crenulated disc.
Left hand example is 46mm long and the right hand 5mm long

DISCUSSION

Class

The class Scaphopoda, with around 1000 living and fossil named forms to classify, can be divided conveniently into the classical three-fold divisions of a class, without the addition of suprageneric taxa of intermediate value. In this it differs from the very much larger molluscan classes where the simple Class-Order-Family-Genus hierarchy requires expansion, with intermediate taxa, in order to cope with all the natural divisions.

Before Pilsbry & Sharp's (1897 - 1898) excellent monograph on the scaphopods these molluscs had suffered a disturbing taxonomic history. They had no fixed name and lived, like outcasts, in the Class Gastropoda (or Gasteropoda). They were accorded status ranging from genus to suborder and were usually found, in the company of a variety of serpulid worms and non-scaphopod molluscs, near to the Patellidae and the Fissurellidae. The names given to them include: Cirrobranchiata Blainville, 1825 to 1832; Lateribranchiata Clark, 1851; Soleneconches Lacaze-Duthiers, 1857; Heteroglossa Gray, 1847; Prosocephala (suborder); and Scaphopoda (order) Bronn, 1862. In 1897 Pilsbry & Sharp rescued them from the gastropods, removed the attendant worms and others and, following Fischer (1885), gave them the full status of a distinct class of the phylum Mollusca, and applied Bronn's name Scaphopoda to it.

Order

At this juncture the Scaphopoda had, so to speak, 'come of age', but in doing so they left a gap at the ordinal level of classification which has subsequently never been filled. Even the latest classification proposed by Emerson passes from the Class Scaphopoda, across the 'ordinal gap', down to the families Dentaliidae and Siphonodentaliidae (Emerson, 1962: 466). It is a fact, which apparently needs stressing, that molluscan workers over the last hundred years have consistently recognised a primary two-fold division of the scaphopod molluscs. Stoliczka (1868) proposed that the family Dentaliidae be split into two subfamilies, Antalinae (p. 437) and Gadilinae (p. 440). Pilsbry & Sharp (1897 - 1898) divided the Scaphopoda into two families, Dentaliidae and Siphonodentaliidae (p. xxix). This arrangement was accepted and retained by Boissevain (1906), Henderson (1920), Grant & Gale (1931), Ludbrook (1960), Fantinet (1959), and Emerson (1962). All recognised that, regardless of the systematic level at which one places the taxon Scaphopoda, the initial division below is two-fold.

Scaphopods have a natural division into two categories: 1) forms with relatively large shells and a conical foot; 2) forms with relatively small shells and a vermiform foot with an expanded, distal, crenulated disc. Since the class status of the Scaphopoda is acknowledged (Pilsbry & Sharp, 1897 - 1898, Ludbrook, 1960, and Emerson, 1962), and it can be demonstrated that these molluscs divide initially into two categories, then no reasonable

objection can be raised to giving this primary two-fold division ordinal rank, particularly when that level is unoccupied. Hence it is now proposed that the first category be named Order **Dentalioida**, and the second, Order **Siphonodentalioida**.

Family

There is no systematic difference between "*Dentalium* sensu lato" (Emerson, 1962: 464) and family Dentaliidae. Both taxa function at the systematic family level and the conventional termination -idae should be applied. It may be that some comfort is to be derived from saying of a badly preserved or broken shell that it is a "*Dentalium* in the broad sense" but the semantic content is identical with the statement that "it is a member of the family Dentaliidae" or "it is a dentaliid scaphopod." All three statements imply that one is not sure of the genus to which it should be referred; and it should be remembered that the broadest use of the term *Dentalium* has been as a synonym of Scaphopoda.

It is therefore proposed that the Order Dentalioida include two families as follows:

1) **Dentaliidae**, here used in a restricted sense to correspond with Emerson's "*Dentalium* sensu lato" plus *Prodentalium* Young, 1942. This family may be defined as including all Dentalioida with a conical foot and shells with longitudinal sculpture;

2) **Laevidentaliidae**, here used to correspond with Emerson's "*Fustiaria* sensu lato" plus *Plagioglypta*. It is defined to include all Dentalioida having a conical foot and shells that are smooth, or with concentric annulations, but lacking longitudinal sculpture.

The Order Siphonodentalioida includes two families as follows:

1) **Siphonodentaliidae**, here restricted to include the genera *Entalina, Siphonodentalium,* and *Pulsellum*. It may be defined to include all scaphopods with a vermiform foot and shells without a constricted anterior aperture.

2) **Cadulidae**, corresponding with "*Cadulus* sensu lato" of Emerson (1962: 464). It is defined to include all scaphopods with a vermiform foot and shells with a constricted aperture in the adult.

Genera

Ludbrook (1960) included only three taxa of generic rank in the family Dentaliidae; these were *Dentalium*, *Plagioglypta*, and *Prodentalium*. Sixteen other named generic groups were placed as subgenera under *Dentalium*. In the Siphonodentaliidae *Cadulus* received six and *Siphonodentalium* two subgenera.

Emerson (1962) placed six generic groups under the taxon "*Dentalium* sensu lato" and eight under "*Fustiaria* sensu lato". If we examine the specific load of living scaphopods alone which these subgenera have to bear it is clear that they are substantial enough to be regarded as full genera, since their morphological distinction from "*Dentalium* sensu stricto" is not disputed. *Dentalium* (s. s.) has about 105 living species (author's unpublished check list), *Fissidentalium* about 40, *Antalis* more than 50, and *Graptacme* about 20. *Tesseracme* and *Coccodentalium* are small but well-defined genera. The number of fossil species of scaphopods which have been described is in excess of 600 and these, even after the most drastic process of 'lumping' has taken place, will further expand the genera in the Dentaliidae very considerably. Taking *Dentalium* (s. s.) as an example, it is possible that this genus might then contain at least 200 living and fossil species of scaphopods.

By modern standards this is an unwieldy number of species for one genus to bear and the position is in no way improved by also including in it *Fissidentalium, Antalis* and *Graptacme*. It is the present writer's view that there is a strong need for dividing *Dentalium* (s. s.) into subgenera, and that "*Dentalium* sensu lato" might have been more appropriately applied to "*Dentalium* sensu stricto" of Emerson's usage. The systematic position in the Laevidentaliidae and Cadulidae is similar but less acute.

It is therefore proposed that the genera included by Emerson (1962) under "*Dentalium* sensu lato" be given full generic rank; that genera included by him under "*Fustiaria* sensu lato" be also given full generic rank, and that genera included under "*Cadulus* sensu lato" be also upgraded to full generic rank, except *Platyschides*.

The changes outlined and proposed above are not so great as they may, at first sight, appear to be. The systematic arrangement is but little altered from that proposed by Emerson – only the systematic level; and the changes of nomenclature are simply those that follow from the changed status of the various taxonomic units.

The overwhelming advantage that follows from upgrading of taxa is that it does allow the class Scaphopoda to expand and occupy all the systematic space that is available to it.

GENERIC GROUPS

Since Emerson's 1962 classification nine new genera have been proposed, one of which, *Progadilina,* is here in-

troduced and described. It is proposed that three others, of pre-1962 date, be brought out of synonymy and put into service, one as a genus and two as subgenera. Of these twelve genera the following are here considered to be insufficiently differentiated from existing genera to be given equal taxonomic rank.

1) *Pictodentalium* Kira, 1959, type species *Dentalium formosum hirasei* [sic] Kira, 1959, for the multicoloured dentaliids including *D. formosum, D. hirasei,* and *D. festivum.* Subgenus of *Dentalium* (s. s.).

2) *Lentigodentalium* Habe, 1963, type species *Dentalium variabilis* Deshayes, 1825, characterised by coloured spots on the ribs. Subgenus of *Dentalium* (s. s.).

3) *Callidentalium* Habe, 1964, type species *Dentalium crocinum* Dall, 1907. The type species of *Laevidentalium, D. incertum,* is an Eocene fossil, while *D. crocinum* is a living form, but it is doubtful whether the distinction between fossil and living species of *Laevidentalium* can be maintained. Subgenus of *Laevidentalium.*

4) *Entalinopsis* Kuroda & Habe, 1957, type species *Dentalium nivosum* Kuroda & Kikuchi, 1933. The type species of *Entalina* is a Neogene fossil with a quadrate apical section, and the apical section of *Entalinopsis* is hexagonal. Subgenus of *Entalina.*

5) *Megaentalina* Habe, 1963, type species *M. teramachii* Habe, 1963, for large pentagonal-sectioned siphonodentaliids. Subgenus of *Entalina.*

6) *Omniglypta* Kuroda & Habe, 1953, type species *Dentalium cerinum* Pilsbry, 1905, for living forms resembling the fossil *Plagioglypta* but with weaker annulations. Subgenus of *Plagioglypta.*

7) *Compressidentalium* Habe, 1963, type species *Dentalium hungerfordi* Pilsbry, 1897, for species of *Fissidentalium* with dorso-ventrally compressed shells. Subgenus of *Fissidentalium.*

The following five genera are added to those recognised by Emerson, 1962.

1) *Paradentalium* Cotton & Godfrey, 1933, type species *Dentalium bednalli* Pilsbry & Sharp, 1897, for the very well defined group of living and fossil species with a hexagonal apex and ribs increasing, more or less, by multiples of six.

2) *Spadentalina* Habe, 1963, type species *Dentalium tubiforme* Boissevain, 1906, for the well defined group of living species with an octangulate sectioned shell at the apex or all along.

3) *Pseudantalis* Monterosato, 1872, type species *Dentalium rubescens* Deshayes, 1825. Here removed from the synonymy of *Fustiaria,* type species *D. circinatum* J. de C. Sowerby, 1823 (Emerson, 1962: 471). *Fustiaria* is useful as the name for the Eocene fossil scaphopods with annulated sculpture and a narrow apical slit, while *Pseudantalis* serves for laevidentaliids with an apical slit but which lack annulated sculpture.

4) ***Progadilina*** Palmer, gen. nov., type species *Dentalium trigonale* Moore, 1866.

Diagnosis: small laevidentaliids with trigonal or quadrate outline and encircling oblique, annulated sculpture over the whole surface of the shell. The first character separates it from *Plagioglypta,* and the second from *Gadilina.*

Holotype and Type Locality: *Dentalium trigonale* Moore, Lower Jurassic, Lower Lias, Oxynotum - Raricostatum zones; excavation for the Gas Works, Gloucester, Glos., England; B. M. reg. no. G 23960, figured Richardson, 1906: 590; plt. 45, fig. 4.

Description: shell small, 10 - 15 mm, slightly but regularly curved, with the ventral (convex) surface bluntly keeled, and the dorsal (concave) surface flattened or slightly concave in section. The whole shell is sculptured with slightly oblique annular ridges, fairly regular in size, and separated by narrow grooves. The annular ridges run obliquely back, from the dorsal to the ventral surface, at a density of about 6 - 8 ridges to the millimeter. The apex is usually broken but some show signs of resorption of the shell, but no sign of a notch or slit. The resorption, together with the regular curvature, indicate that these are true scaphopods and not serpulid worms.

5) *Sagamicadulus* Sakuri & Shimazu, 1963, type species *Striocadulus (Sagamicadulus) elegantissimus* Sakuri & Shimazu, 1963. It is distinguished from the striated *Striocadulus* by the presence of three pairs of apical notches (Sakuri & Shimazu, 1963: 250). Although proposed as a subgenus of *Striocadulus* it is here considered to be a distinct genus since the same order of difference separates *Polyschides* from *Gadila,* and *Siphonodentalium* from *Pulsellum* – the presence of apical notches.

Emerson, 1962, gave *Polyschides* and *Platyschides* equal rank as subgenera of *Cadulus* sensu lato. The latter is distinguished from the former only by the depth of its apical notches. As Emerson (*op. cit.*: 479) points out "The biological significance of this group is questionable. The apical features [of *Platyschides*] nearly approach

those of *Polyschides*." It is therefore proposed that *Platyschides* be used as a subgenus of *Polyschides*.

The foregoing changes reflect advances made in the study of scaphopod molluscs during the decade since Emerson proposed his 1962 classification. By combining these advances with the main body of Emerson's work the following classification results.

Proposed Classification of the Scaphopod Mollusca

Class SCAPHOPODA Bronn, 1862

Order **DENTALIOIDA** Palmer, ord. nov.

Family DENTALIIDAE Gray, 1847

Genus *Dentalium* Linnaeus, 1758; type species *D. elephantinum* Linnaeus, 1758

Subgenus *Pictodentalium* Kira, 1959; type species *D. formosum* Adams & Reeve, 1848

Subgenus *Lentigodentalium* Habe, 1963; type species *D. variabilis* Deshayes, 1825

Genus *Paradentalium* Cotton & Godfrey, 1933; type species *D. bednalli* Pilsbry & Sharp, 1897

Genus *Spadentalina* Habe, 1963; type species *D. tubiforme* Boissevain, 1906

Genus *Tesseracme* Pilsbry & Sharp, 1898; type species *D. quadrapicale* G. B. Sowerby, 1860

Genus *Coccodentalium* Sacco, 1896; type species *D. radula* Schröter, 1784

Genus *Prodentalium* Young, 1942; type species *P. reynardi* Young, 1942

Genus *Fissidentalium* Fischer, 1885; type species *D. ergasticum* Fischer, 1882

Subgenus *Compressidentalium* Habe, 1963; type species *D. hungerfordi* Pilsbry & Sharp, 1897

Genus *Compressidens* Pilsbry & Sharp, 1897; type species *D. pressum* Pilsbry & Sharp, 1897

Genus *Antalis* H. & A. Adams, 1854; type species *D. entalis* Linnaeus, 1758

Genus *Graptacme* Pilsbry & Sharp, 1897; type species *D. eboreum* Conrad, 1846

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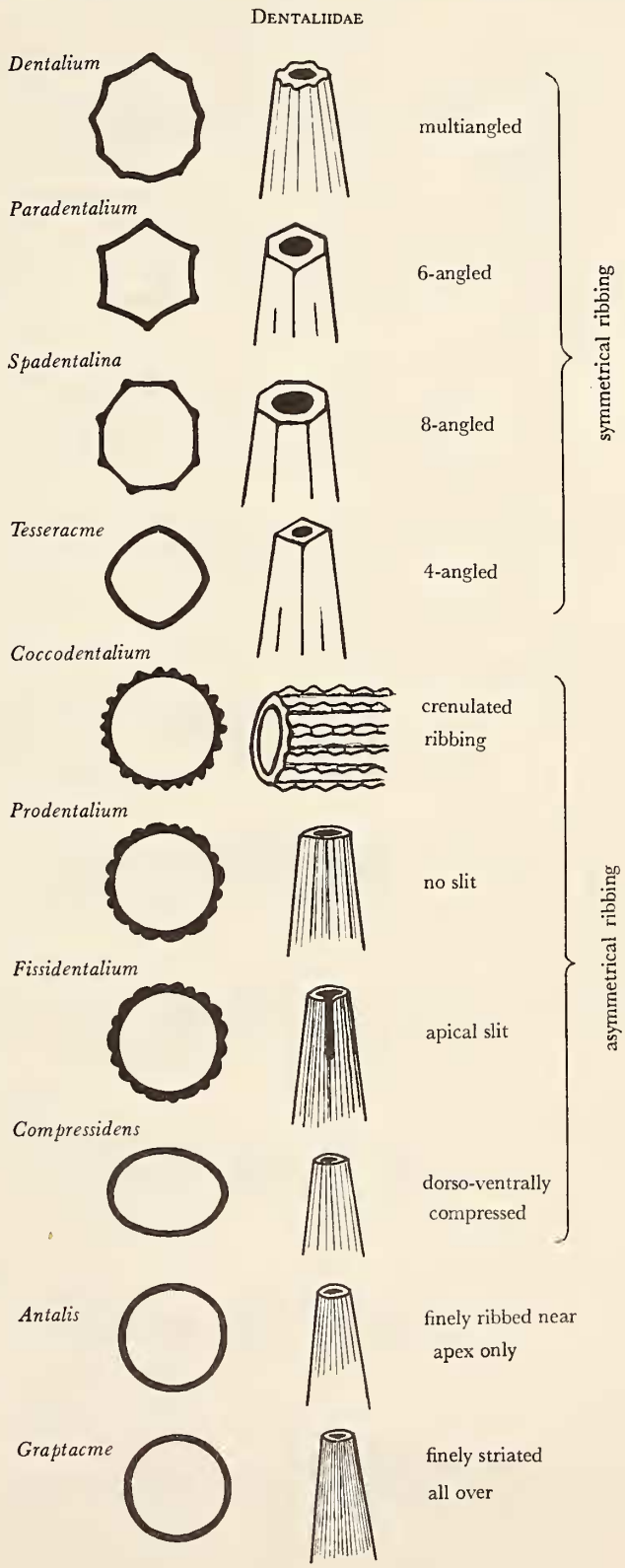
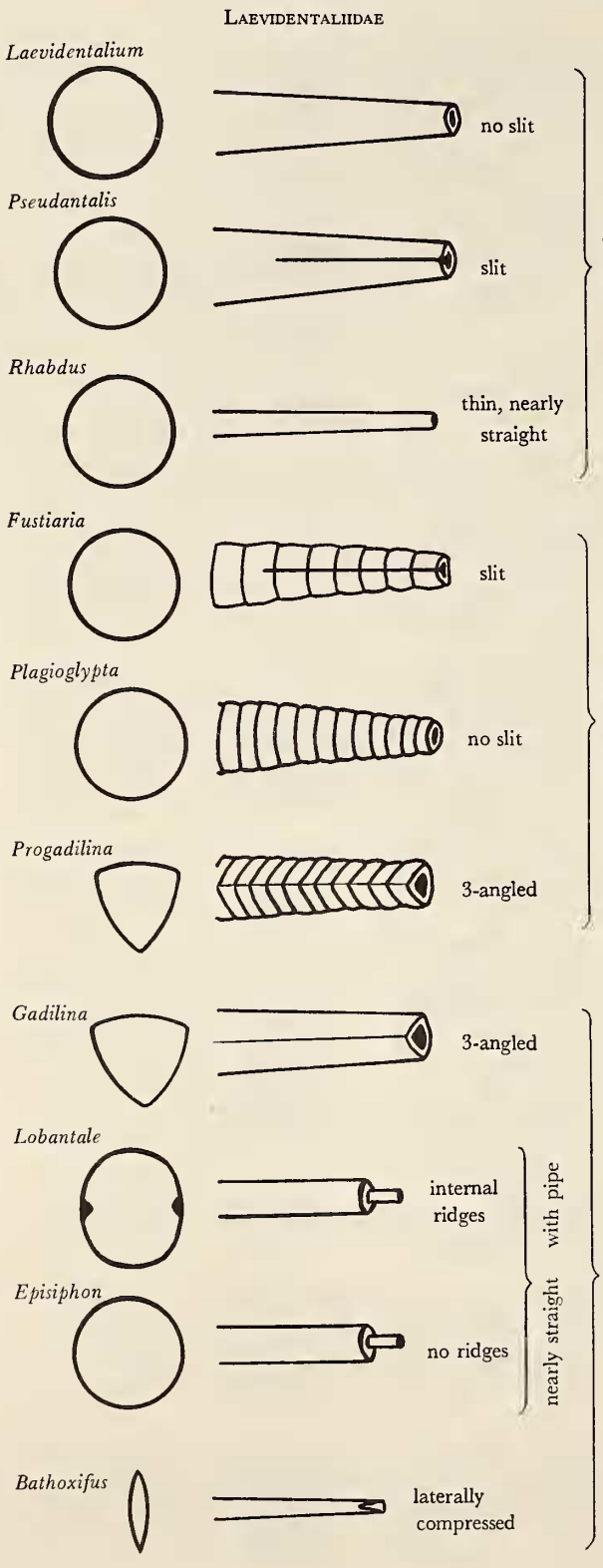


Figure 2

Genera of the Dentaliidae
left hand figures represent cross sectional shape at the aperture; right hand figures show apical characters. All figures are diagrammatic and not to scale



Family Laevidentaliidae Palmer, fam. nov.

Genus *Laevidentalium* Cossmann, 1888; type species *D. incertum* Deshayes, 1825

Subgenus *Callidentalium* Habe, 1964; type species *D. crocinum* Dall, 1907

Genus *Pseudantalis* Monterosato, 1872; type species *D. rubescens* Deshayes, 1825

Genus *Rhabdus* Pilsbry & Sharp, 1897; type species *D. rectius* Carpenter, 1865

Genus *Fustiaria* Stoliczka, 1868; type species *D. circinatum* J. de C. Sowerby, 1823

Genus *Plagioglypta* Pilsbry & Sharp, 1897; type species *D. undulatum* Münster, 1844

Subgenus *Omniglypta* Kuroda & Habe, 1953; type species *D. cerinum* Pilsbry, 1905

Genus ***Progadilina*** Palmer, gen. nov.; type species *D. trigonale* Moore, 1866

Genus *Gadilina* Foresti, 1895; type species *D. triquetrum* Brocchi, 1814

Genus *Lobantale* Cossmann, 1888; type species *D. duplex* DeFrance, 1819

Genus *Episiphon* Pilsbry & Sharp, 1897; type species *D. sowerbyi* Guilding, 1834

Genus *Bathoxifus* Pilsbry & Sharp, 1897; type species *D. ensiculus* Jeffreys, 1877

Order **SIPHONODENTALIOIDA** Palmer, ord. nov.

Family SIPHONODENTALIIDAE Simroth, 1894

Genus *Entalina* Monterosato, 1872; type species *D. tetragonum* Brocchi, 1814

Subgenus *Entalinopsis* Kuroda & Habe, 1957; type species *D. nivosum* Kuroda & Kikuchi, 1933

Subgenus *Megaentalina* Habe, 1963; type species *M. teramachii* Habe, 1963

Genus *Siphonodentalium* M. Sars, 1859; type species *D. lobatum* G. B. Sowerby, 1860

Genus *Pulsellum* Stoliczka, 1868; type species *D. lofotense* M. Sars, 1865

(← adjacent column)

Figure 3

Genera of the Laevidentaliidae

left hand figures represent cross sectional shape at the aperture; right hand figures show apical characters. All figures are diagrammatic and not to scale

Family Cadulidae Grant & Gale, 1931

Genus *Cadulus* Philippi, 1844; type species *D. ovulum* Philippi, 1844
Genus *Gadila* Gray, 1847; type species *D. gadus* Montagu, 1803
Subgenus *Gadilopsis* Woodring, 1925; type species *Ditrupa dentalina* Guppy, 1873
Genus *Dischides* Jeffreys, 1867; type species *Ditrupa politus* S. V. Wood, 1842
Genus *Polyschides* Pilsbry & Sharp, 1898; type species *Cadulus tetraschistus* Watson, 1879
Subgenus *Platyschides* Henderson, 1920; type species *Cadulus grandis* Verrill, 1884
Genus *Striocadulus* Emerson, 1962; type species *Cadulus albicomatus* Dall, 1889
Genus *Sagamicadulus* Sakuri & Shimazu, 1963; type species *Striocadulus (Sagamicadulus) elegantissimus* Sakuri & Shimazu, 1963

Good figures of the type species will be found in the following publications: Pilsbry & Sharp, 1897 - 1898; Boissevain, 1906; Richardson, 1906; Henderson, 1920; Emerson, 1962; Kira, 1962; Sakuri & Shimazu, 1963; Habe, 1963; Habe, 1964.

Addendum in Proof

Calstevenus Yancey, 1973; Journ. Paleontol. 47 (6): 1062 - 1064. Type species *C. arcturus* Yancey, 1973, *op. cit.*: 1063. This was described as a siphonodentaliid scaphopod from the Permian, Wolfcampian; Rieptown Formation of the Arcturus Group; from the western part of White Pine County, Nevada, U. S. A. Since it lacks a constricted aperture it should be included in the Siphonodentaliidae of the present classification.

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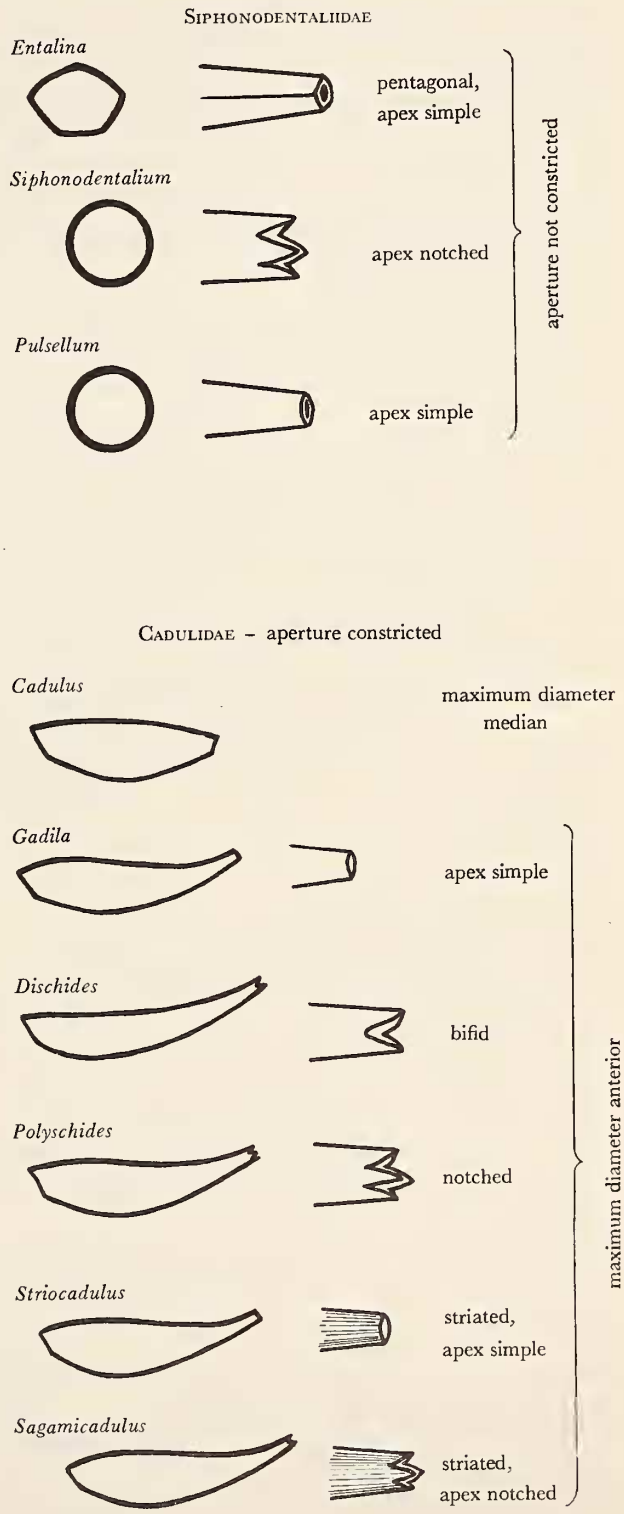

Figure 4

Genera of the Siphonodentaliidae and Cadulidae
Left hand figure in the Cadulidae is the lateral view of the shell; right hand figures show apical characters. All figures are diagrammatic and not to scale

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